



Flowers: Plant Evolution's Most Valuable Invention *by Glenn Keator*

Before flowering plants, the world was a much drabber place with few splashes of color beyond the greens, grays, browns, and blacks of the conifers and “lower” plants like ferns, mosses, and liverworts. Food for browsers was much more limited in concentrated energy—for example, sugars—and few mammals or advanced insects existed. So what is special about flowering plants and how did they originate?

The last part of the question is still very much debated, for no convincing fossils show intermediate forms between extinct gymnosperms like the seed ferns and the true flowers. We do have several living candidates whose DNA suggests great age, but that’s about it, and ideas of what the first flowers were like keep changing, with many earlier theories debunked.

What is a flower? You’ll find many definitions of a flower, but the essence of flowerhood is the ovary, a hollow vessel that contains the future seeds, protecting them and allowing a long development before the ripe seeds make their own way into the world. Other flower traits include stamens, the producers and containers of pollen grains, which are moved to the stigma above the ovary during pollination. This process involves a wide range of wondrous animals and, sometimes, wind or water. Still other

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definitions include the details of fertilization, from the tiny *embryo sac* hidden inside each putative seed to the formation of the nutrient tissue for the seeds' embryos, the *endosperm*.

What fascinates me is the unparalleled diversity of flowers, their range of sizes from pinhead to dinner plate, the rainbow of colors and color patterns, the fragrances, the rewards offered to pollinators such as nectar and pollen, and the fruits that result: dry capsules, hard nuts, feathered achenes, and all manner of brightly colored fleshy berries and drupes, for seed dispersal is as varied and resourceful as pollination.

And what is the purpose of flowers? All the colorful ones have the single purpose of promoting pollination, leading to fertilization of the ovules' eggs. But there are others: flowers without petals, nectar, or fragrance, honed to the minimum necessary parts—stamens and pistils—and thus dependent on the wind. Although beginning botanists laud the efficiency of animal pollination, some of our most successful plants such as the vast grass family (Poaceae), and trees such as maples, oaks, and birches, are all highly successful by simply using the wind.

The Timeline For a Typical Flower

- The bud stage, flowers first forming when conditions are right (Inside the buds, preparations are made so that when the flower opens it's ready for pollination.)
- Anthesis, the open flower, usually consisting of protective sepals, colored petals, stamens, and pistils, the latter made up of the ovary, style, and stigma (Anthesis is when pollination occurs and flowers make their best displays.)
- Pollination, the transferring of pollen from the stamen to the stigma, usually from one flower to a different one on a different plant (cross pollination)
- Withering of flower parts, the petals and stamens usually shed
- Growth of pollen tubes, from the stigma down the style and into the ovary, each tube finding a potential match with an ovule (the preformed seed)
- Double fertilization, the pollen tube releasing two sperms, one to fuse with an egg in the ovule, the other to join with the polar nuclei inside the embryo sac of the ovule
- Seed growth, with the fertilized egg forming

an embryo plant and the ovary changing size and form as the seeds inside mature

- The ripening of the ovary into a fruit and the release and dispersal of seeds

Examples abound in California's diverse flora, illustrating modifications to flowers that serve to attract pollinators: shape, color, odor, and rewards.

Flower Shape—an Important Determinant to Pollinator Access

Wide-open, often symmetrical, flowers are generalists, inviting visits from a wide array of potential pollinators, offering up shallow saucers and cups with ample landing platforms on the petals and easy access to nectar. Others provide tiny flowers, massed into heads or flat-topped clusters. These unspecialized flowers offer free lunches. The disadvantage of this design? Free rewards for visitors whether they pollinate or not.

Some specialized flowers feature long tubes, hiding nectar inside, or attractive asymmetrical flowers, or male and female flowers on separate plants, and a variety of other methods to avoid self-pollination.

Flower Color—a Fascinating Insight into Luring Pollinators

In the spring, the majority of flowers are yellow, blue, purple, or white, colors attractive to bees, whose vision is strong in yellows, blues, and purples, or combinations of these. White flowers often have a hidden-to-our-eyes ultraviolet color, attractive to bees as well. Ultraviolet-sensitive film will reveal a pattern we can't see that acts as nectar guides in the form of dots, lines, and blotches, that, for example, make many yellow daisies look different to bees.

Flower pigments are often complex mixtures rather than a single color, and bees easily see yellow in orange flowers such as California poppy. By contrast, red is seldom noticed by bees, although some insects, like butterflies, see shades of red-purple and pink. However, the main contenders for red flowers are

Glenn Keator



California fuchsia (*Epilobium septentrionale*), with trumpet-shaped scarlet flowers and protruding stamens indicating hummingbird pollination. Note that both sepals and petals are brightly colored.

hummingbirds, which, incidentally, see other colors equally well.

So it's a mystery to people when they see bees approaching red flowers like columbine (*Aquilegia formosa*) or California fuchsia (*Epilobium canum*). The reason? These flowers also have yellow pigments.

Odor—Usually Obvious to Our Noses

While bees and many other insects, most especially sphinx moths, are strongly

attracted by sweet odors, hummingbird flowers lack odor because these birds have no sense of smell. Unpleasant, acrid, stinky, putrid, and other odors like rotting fruit attract still other pollinators, including many kinds of beetles and flies and, in the case of rotting fruit like spicebush flowers (*Calycanthus occidentalis*), beetles that typically feed on decaying fruits. Wind-pollinated flowers produce no odor.

Finally, Rewards that Keep Pollinators Visiting—Nectar and Pollen

Nectar, although always a combination of certain sugars and water, varies with respect

to the kinds of sugars, their concentration, and other components like amino acids. Copious nectar, for example, is provided for hummingbird visits. Most flowers have *nectaries*, special organs that release nectar located at the base of petals, sepals, and sometimes on the lower end of ovaries. This positioning is part of the success of specific pollinators that visit specific flowers.

Extra pollen is important in nourishing young bees. Pollen-only flowers produce a great excess of pollen, usually through numerous stamens, and are typical of most of the poppy family (Papaveraceae).

Then there are the flowers that lure pollinators without giving a reward—false advertising in the plant world. For example, the unique flower of California pipevine (*Aristolochia californica*) uses color and odor to lure tiny midges inside to be trapped temporarily. The midges deposit pollen or pick up new loads of pollen before the flower

Arlyn Christopherson



California pipevine (*Aristolochia californica*), "mouth" open, inviting pollinating midges

opens enough to let them make an easy exit. In fact, at one time, trap flowers were thought to digest their "prey" for food, but only the leaves of *insectivorous* plants "eat" their prey for nutrients.

Examples of Flower Strategies for Pollination

Not all petaled flowers present a uniform, symmetrical pattern, and some that do are reduced to tiny sizes that are massed together for an easy-to-see effect from afar. Among such flowers we find our lovely wild lilacs (*Ceanothus* spp.), whose sepals and petals are both colored,



Jepson ceanothus (*Ceanothus jepsonii*), a low-growing shrub from the North Bay, showing the nature of the flower structure, the sepals and petals both colored

Pattie Litton



Western spicebush flower (*Calycanthus occidentalis*) showing an indefinite number of spirally arranged red tepals attractive to beetles



Naked-stem buckwheat (*Eriogonum nudum*), with wide open flowers featuring tepals that start white and turn pink with age, indicating whether nectar is available or not

the dense clusters of flowers providing the incentive to visit. Such is also the case with wild buckwheats (*Eriogonum* spp.) and many members of the rose family (Rosaceae), like the spiraeas (*Spiraea* spp.), chamise (*Adenostoma fasciculatum*), and mountain mahoganies (*Cercocarpus* spp.).

In some groups, many tiny flowers are massed together to resemble a single large, showy flower. The premier example is the enormous daisy family (Asteraceae), where many species have petallike ray flowers around a dense head of tiny disc flowers, the rays providing a landing platform for bees, the disc flowers carrying the burden of producing pollen, nectar, and stigmas to make seeds.

Unrelated, but using the same design principle, is our flowering dogwood (*Cornus nuttallii*), whose large flower is actually a collection of white petallike bracts around a head of tiny, green flowers. Another similar wrinkle is used by western skunk cabbage (*Lysichiton americanus*), whose apparent flower is actually a spike of many petalless white flowers surrounded by a showy, yellow *spathe bract*, resembling an oversized petal.

Many other tiny typical flowers are massed together in heads or flat-topped clusters, providing ample places for pollinators to land, the flowers wide open with nectar available to all. Examples include yarrow (*Achillea millefolium*), cow parsnip (*Heracleum maximum*),

and many other members of the parsley family (Apiaceae).

Long tubular flowers, worked only by long-tongued pollinators like hummingbirds, butterflies, and bumblebees, whose beaks and tongues are long enough to reach their reward, often extend their stamens and stigmas for effective contact with the pollinators' bodies. Similar in effect are flowers with tapered nectar spurs such as columbines (*Aquilegia* spp.) and larkspurs (*Delphinium* spp.). For two-lipped flowers, pollinator selection depends on the length of the petal tube, shallow ones favoring bees, longer ones other pollinators, except in the cases where the petal tube is broad enough for pollinators to crawl inside.

Asymmetrical flowers are often claimed to be more enticing to bees than the symmetrical kinds. In this category belong myriad examples, some like the violets (*Viola* spp.) have unjoined but unequal petals, while others like the sages (*Salvia* spp.), pitcher-sages (*Lepechinia* spp.), penstemons (*Penstemon* spp.), and Chinese houses (*Collinsia* spp.) sport two lipped flowers, where petals are joined to form a tube that ends in two sets of lobes: the lower lip of three lobes, the upper of two.



Cow parsnip (*Heracleum maximum*), showing wide-open flowers. The white color probably has invisible ultraviolet markings.



Red tubular flowers of hummingbird sage (*Salvia spathacea*) with protruding stamens pollinated by hummingbirds

While typical flowers have green sepals and colored petals, many of our lily relatives sport colored sepals *and* petals, the two whorls of the flower resembling each other in color and shape, providing a double row of attractive parts. In this group, we find lilies (*Lilium* spp.), fritillarias (*Fritillaria* spp.), wild onions (*Allium* spp.), and many more.

Within the groups with colored sepals and petals, the two parts may differ in size and shape while both provide color signals to pollinators. Perhaps no other group is more interesting in this regard than irises (*Iris* spp.), whose flowers have an intricate mechanism to ensure cross-pollination. The three petallike sepals provide a landing platform for pollinators, with colored lines that serve as nectar guides. The petals, by contrast, stand stiffly upright, while a third apparent row of petals in the flower's center represent style branches, each branch tip carrying a tiny flap of stigmatic tissue underneath. The three stamens are positioned out of sight between each sepal and style branch, and all are attached to the top of a nectar tube or *hypanthium*. Now the stage is set for bee visitation, the bee landing on a sepal and, while following the nectar guides, brushing against the stigma, followed by an encounter with a stamen before reaching the nectar-rich hypanthium. Since the stigma can bend in only one direction, the new load of pollen is not transferred to the same flower as the bee exits but is carried to a new flower to repeat the process.

Larkspurs (*Delphinium* spp.) provide another good example of different-looking colored sepals and petals. The sepals are showy, the upper one extending back into a tapered nectar spur, while the petals are smaller and hide the stamens.

Sometimes the transition to flowers with either sepals or petals missing clearly shows what may happen in the evolutionary process. Monkshood (*Aconitum columbianum*) represents this trend: the sepals are colored and petallike, but the petals are modified into nectar-bearing spurs hidden inside the upper sepal or hood.

Many flowers have lost part of the *perianth*, either the sepals or petals, the remaining parts colored and attracting pollinators. Examples here include our beautiful fremontia (*Fremontodendron* spp.), buckwheats (*Eriogonum* spp.), and marsh marigold (*Caltha leptosepala*).

Still other flowers retain only sepals, the sepals their usual green color, a phenomenon encountered in such wind-pollinated flowers as mountain meadow rue (*Thalictrum fendleri*), where colored parts are no longer needed to attract pollinators.

Along this same line, we find most wind-pollinated flowers even more streamlined, lacking sepals or petals, and bearing bracts below stamens or pistils, the two often on



Monkshood (*Aconitum columbianum*), the only species of monkshood in California, showing the hooded upper sepals and the many stamens

Arlyn Christopherson



Arroyo willow (*Salix lasiolepis*), male catkins with petal-less wind-pollinated flowers showing yellow stamens

Arlyn Christopherson



Big leaf maple (*Acer macrophyllum*) flowers

Arlyn Christopherson



Box elder (*Acer negundo* var. *californicum*), petalless male flowers

separate plants (*dioecious*) to avoid self-pollination. In this category belong willows (*Salix* spp.) and the evergreen silk-tassel bush (*Garrya* spp.). *Monoecious* plants—flowers of both sexes on the same plant—include sycamore (*Platanus racemosa*), oaks (*Quercus* spp.), and alders (*Alnus* spp.). Such plants avoid self-pollination by producing the male and female stages at different times.

Also wind-pollinated, the huge grass family (Poaceae) and the sedge family (Cyperaceae), though not woody, grow in great stands enabling wind to effectively move pollen from plant to plant. Here the tiny flowers consist of bracts below extended stamens and feathery stigmas, the male part releasing pollen before the female part is ready to receive it, reducing the chance for self-pollination. These families are considered more recently evolved, not basal groups that first arose among the flowering plants. Intermediate stages for this phenomenon can occur within a single genus, like the maples (*Acer* spp.): big-leaf maple (*A. macrophyllum*) has colored petals, while box elder (*A. negundo*) lacks petals altogether, demonstrating that petaled ancestors often lead to wind-pollinated flowers through elimination of the perianth.

The ultimate reduction of flowers is provided by the tiny floating aquatics known as duckweed (*Lemna*, *Wolffia*, and *Wolffiella* spp.), where the main mode of reproduction is the breaking off of tiny side branches—the flowers only occasionally appear, apparently under stressful conditions, each flower a minute stamen or a tiny pistil and nothing more.

These examples could be expanded indefinitely for the thousands of California natives, often providing surprises and new wrinkles on the evolutionary scene. Our awareness of these important ways of viewing flowers will provide hours of inquiry and pleasure. 🌿

Glenn Keator is chair of the Friends Advisory Council. He is a popular instructor of botany and field trip leader in the Bay Area and teaches the docent training course at the Regional Parks Botanic Garden. He is the author of a number of books on native plants.

The Buzz in My Garden *by May Chen*

Ever since the chaparral nightshade (*Solanum xanti*) was planted in my garden it has never stopped blooming. While I begrudge the plant's aggressive spread, I appreciate the year-round show of color and the population of bumblebees and carpenter bees it sustains. Best of all, it affords me a front row seat to *buzz pollination*, much loved by pollination observers.

What is buzz pollination?

Solanum flowers are often used as the standard model for the study of buzz pollination, or *sonication* as some prefer to call it. The tubular anthers are clustered in the center of the open-faced flower, forming an anther cone surrounding a sturdy style. These anthers are *poricidal*, that is, they have a tiny opening or pore at their tip through which pollen is expelled. When the flower is shaken or vibrated at the appropriate frequency, the dry pollen is released through the pores, similar to the way salt shakers work. *Solanum* flowers tend to nod or face downward, so pollen release is aided by gravity as well.

Ted Muller



Nightshade (*Solanum* sp.)

How does sonication work? When a bumblebee attempts to collect pollen from a *Solanum* flower, it grasps the anther cone with its legs or mouthparts. Hanging upside down, the bee decouples its wings from its flight muscles in its thorax, so that when it vibrates those flight muscles, the wings don't move, but its body vibrates violently. The bee's buzz

suddenly shifts from the low hum typical of flight to a fevered high pitch. The change in pitch is readily audible to a human listener. The vibration shakes the pollen out of the anthers onto the bee's body. Very efficiently, the bee grooms the pollen into its *pollen baskets*, a pair of structures on its hind legs for transporting pollen to the hive. On subsequent visits to other flowers of the same species, the pollen that remains on its body might rub off on the protruding stigma, effectively pollinating the flower.



Bumblebee (*Bombus* sp.) sonicating a tomato flower. The dark bruises on the anther cone of the upper flower, referred to affectionately as "bee kisses" by pollination biologists, indicate that the blossom has been buzz-pollinated.

During sonication *Solanum* flowers are shaken by bees with forces approaching three Gs—the equivalent of an astronaut blasting into space. Both flower and bee must be adapted to withstand these forces. Not all bees are capable of buzz pollination. Interestingly, while the honey bees are known for their versatile pollination habits, they are not capable of sonication. The technique is used mainly by bumblebees, carpenter bees, and some stingless bees and sweat bees. Pollen transfer during sonication is aided by electrostatic attraction. When a bee is flying, it acquires a slight positive charge as electrons are stripped from its body as it collides with air particles. Flowers (and plants in general) being grounded, have a slight negative charge. Pollen

grains have been shown to literally jump onto a bee's hairs before direct contact is made.

In the bee species that sonicate, buzz pollination is probably an innate behavior, as the insects exhibit sonication on their first foraging trips. However, there is also a learned component—bees improve their sonication technique over several days of foraging.

Convergent Traits

Approximately six to eight percent of flowering plants are dependent on buzz pollination, many from unrelated families. These represent one of the first-recognized examples of convergent evolution in floral morphology. Traits shared by these flowers include: pendant flowers, radial symmetry, reflexed petals, prominent cone of stamens with short robust filaments and poricidal anthers, a simple style that protrudes from the tip of the anther cone, and an absence of nectar. Another prominent example of a buzz-pollinated flower in our native flora that possesses these *solanoid* traits is the shooting star (*Primulus* [*Dodecatheon*] spp.) in the primrose family (Primulaceae).

Manzanita Mystery

I have often observed bees buzzing manzanitas (*Arctostaphylos* spp.) in the wild, but when the manzanitas in my own garden started to bloom this winter, I began to pay close attention. From the high-pitched buzz they produce at the flowers, there's no doubt in my mind that the bumblebees are sonicating the flowers. But other than the pendant flowers, there's no obvious resemblance between these tiny urn-shaped flowers and the open-faced blossoms of the nightshade.

Finally, I decided to investigate for myself. I sonicated a manzanita flower by striking a middle C tuning fork and placing it near the flower, meanwhile holding a piece of index card underneath. To my disappointment, no visible cloud of pollen fell out. I did notice, however, a few minute, pale flecks falling on the paper. I collected a couple of the flowers and dissected them under the microscope. On close inspection, the manzanita flower began to disclose some of its secrets. Indeed, it has poricidal anthers—about ten of them arranged in a circle around a sturdy style that extends to the opening of the urn-shaped corolla, the latter made up of fused petals. The pores were huge relative to the size of the paired anthers—their gaping maw revealed no pollen within. Apparently, the pollen

had all been emptied out. Rather striking was the pair of horn-like appendages on the back of the anthers. And there was a dense forest of fine hairs extending from the swollen bases of the stamens. A couple of drops of liquid glistened as I parted the stamens with a fine probe—was this nectar perhaps?



David Nelson

Longitudinal section of a manzanita flower

As I continued to observe the bees visiting the manzanita, the internal floral structures began to make sense. Since the flowers are too small to admit most larger bees, the bees sonicate them from the outside, sometimes even grasping a few adjacent flowers in a cluster while simultaneously buzzing. Perhaps those appendages on the anthers serve to enhance contact with the corolla and thereby help transmit the bee's vibration to the anthers. The dense hairs at the base of the stamens may serve to protect the nectar from small crawling insects that manage to get in, but do not serve as pollinators.

I am intrigued by close-up photos of manzanita flowers that have been perforated with holes. The holes are chewed or cut by *nectar robbers*, bees or other insects that attempt to gain direct access to the nectar without entering the flower. Since they do not directly contact the flower's sexual parts,

Christine Casey/Häagen-Dazs
Honey Bee Haven



Honey bee probes for nectar with its tongue.

these robbers do not contribute any pollination service to the plant. What's more, secondary robbers are often seen sipping at the holes, taking advantage of ready-made openings. It's a jungle out there!

Honey bees often visit the manzanita, hanging from the flowers. Not able to sonicate, they probe for nectar with their long tongues. In doing so, they may jostle the anthers enough to release some pollen onto their bodies. Honey bees also feed at perforations at the base of the flowers, nectar robbing—tsk, tsk!

What about those minute flecks that fell out of the flowers I sonicated? Under the microscope, they revealed themselves to be nymphal or immature thrips, still incapable of flight. What in the world are they doing in the manzanita flowers?

Thrips (order Thysanoptera) are minute (most are one millimeter or less), slender insects with fringed wings and unique asymmetrical mouthparts that they use to feed on plant tissues by puncturing and sucking the contents. They are feeble flyers, but capable of long-distance travel aided by air currents. Their feeding habits and their ability to transmit viral diseases to their host plants have earned them a reputation as plant pests. Yet some thrips are known to be effective pollinators. I was thrilled to learn a new word, *thripophily*. The term refers to a suite of characteristics of flowers pollinated by thrips, including: flowers small- to medium-sized; petals white to yellow or greenish, often tipped with pink; pleasantly scented; sometimes borne in compact blossoms; sometimes in the form of sheltering globose or urceolate (urn-shaped) flowers; blossoms providing minute quantities of nectar; and small- to medium-sized pollen grains. The manzanita flower seems to fit the bill!

Generally male and female thrips visit flowers cued by scent, color, and possibly form. They feed on pollen

and mate. Females proceed to lay eggs on the spot or on subsequent flowers they visit. Larvae that hatch out eventually drop to the ground to pupate. Adult thrips bearing pollen grains breed in the flowers of many plant species and contribute to their pollination. The phenomenon is well studied in the cycads. A 2015 study of pointleaf manzanita (*Arctostaphylos pungens*) concluded that thrips do pollinate the manzanita and do contribute significantly to the reproductive success of the plant.

While winter is hardly the time to see insects, it is not uncommon to spot a butterfly visiting the manzanita for nectar on a sunny day. The butterfly is most likely one of the following species: mourning cloak, painted lady, red admiral, tortoiseshell, or monarch butterfly. Why? These species brave the winter as adults while most others are hidden out of sight as caterpillars or chrysalids through the cold, wet season.

Many of our Anna's hummingbirds no longer migrate. Why bother when they can hang around nectar feeders in gardens and occasionally sip nectar from manzanita blossoms through the winter?

Manzanitas exhibit a generalist pollination strategy. While sonication is probably its most effective mode of pollen transfer, the plant is visited by an amazing diversity of insects, legitimate pollinators or not. Blooming in winter and early spring, when few other floral resources are available, manzanitas provide pollen and nectar as well as shelter and breeding sites for many. Insect activities not only support the plant's own reproductive agenda, but also the survival of the animals that depend on it. We must not forget that the results of pollination—the berries or "little apples" that give manzanita its name—go on to provide food for mammals and birds as well.

Like many gardeners, I planted manzanitas mainly for their beautiful mahogany bark, their graceful branching patterns, and their evergreen foliage. Little did I realize the important role they play in the larger ecological context. Viva Manzanita! 🌱

As a docent at Audubon Canyon Ranch for the last 23 years, **May Chen** leads hikes for children at Martin Griffin Preserve. She is also a volunteer with the Friends of Sausal Creek in Oakland, helping with plant propagation in their nursery and tending the pollinator garden. She gives talks and leads field trips for school children and adults who seek out her expert and entertaining insights into plants and their pollinators.

Marc Kummel



Tiny thrips on bigberry manzanita (*Arctostaphylos glauca*)

Propagation Notes *by Susan Ashley*

Jeweled Onion (*Allium serra*)

The jeweled onion is at home on clay and serpentine soils, favoring grassy slopes in the foothills and valleys surrounding the San Francisco Bay and in the Coast Ranges of central and northern California. It has bright pink flowers on 4- to 15-inch stems, iridescent when first opening, then becoming papery with age. It flowers from March to May depending on elevation. An unusual feature of the jeweled onion, and a useful tool in identification, is the minute herringbone pattern on the surface of the bulb.

Although most sources say no treatment is needed to germinate the seeds, California wild onions benefit from six weeks to three months of cold stratification. One can also sow outdoors in fall if you live in an area that gets below 45 degrees Fahrenheit for several months in winter. Germination will take place in early spring. Transplant seedlings when about three inches tall. They will form a bulb the first year and bloom the second year, becoming deciduous perennials.

Plants have at times been listed for sale at East Bay Wilds in Oakland, California. No seed sales have been located. Many beautiful native onions can be purchased from Telos Rare Bulbs (telosrarebulbs.com). Onion flowers will produce abundant seed that can be collected and sown.



Jeweled onion (*Allium serra*)

Arlyn Christopherson



Crimson columbine (*Aquilegia formosa*), showing the red spurs where nectar is held

Crimson Columbine (*Aquilegia formosa*)

A widespread species, the crimson columbine grows from Alaska all the way south to Baja, and eastward to the foot of the Rockies. It is found below 10,000 feet but not in the Central Valley or low desert regions. It is a winter-deciduous perennial and blooms from April to August depending on location and moisture. The wiry two-foot stems carry several coral and yellow flowers attractive to hummingbirds and often pollinated by sphinx moths. Happiest in moist part shade, crimson columbine is found growing along streambanks in oak woodlands, chaparral, and mixed evergreen and coniferous forests. It is an easy garden subject, often self-seeding but sometimes suffering from mildew at the end of the season. Successful seed germination is greatly increased by six weeks of cold stratification. (Sowing outdoors in fall will achieve the same result, but requires months instead of weeks.) When seedlings have several sets of true leaves, they may be transplanted into pots and allowed to grow until they are large enough to survive in the ground (usually when roots reach the bottom of the container, visible if you gently tip the plant out of the pot). Crimson columbine seeds can be found online or in the seed box in the Regional Parks Botanic Garden Visitor Center. The seeds are poisonous.

Wind Poppy (*Papaver heterophyllum*)

During the superbloom spring of 2017, long-

Wind poppy (*Papaver heterophyllum*)

quiescent populations of wind poppy blanketed slopes from the Bay Area south to the Mexican border, in the coastal ranges and Sierra foothills, blooming in April and May with papery orange blossoms whose crimson centers are ornamented with showy yellow stamens. The slender 18-inch stems wave in the wind. It is an easy garden annual and makes a

good oak understory, blooming in sun or part shade. Easy to germinate, it needs no special treatment and can be broadcast on bare soil in fall and germinated by the rains. It is delicate to transplant. If sown in a container it is best sown in individual cells, a few seeds per cell, and transplanted as a whole when the roots fill the container enough to stay together when the plant is tipped out. Fall sowing will produce a much larger plant with showier flowers than spring sowing. The plant will go to seed and come back in subsequent years if the competition is kept at bay. Minimal irrigation will prolong the bloom. The seed is available at the Botanic Garden Visitor Center and sometimes online, and plants can be found in spring at Annie's Annuals and Perennials in Richmond, California.

Glandular Clarkia (*Clarkia arcuata*)

There are 40 species of clarkias, almost all native to western North America. All are annuals with four petals and four sepals, growing in great swaths of red, pink, purple, or white, with many bicolored species. *Clarkia arcuata* blooms from April to June in the foothills of the Cascade Range and the north and central Sierra Nevada below 5,500 feet. It tolerates serpentine soils and is commonly found in openings in woodlands or chaparral, growing to about 15 inches. The petals are purplish pink and covered in glandular hairs, thus the common name. The Botanic Garden has a rare pale pink form with petals fading to white in the center. Propagation of the glandular clarkia is the same as for mountain garland, the clarkia found in the next entry.

Mountain Garland (*Clarkia unguiculata*)

Widely distributed from the North Coast Ranges south to the Tehachapi Mountains, and the southern Sierra Nevada foothills, the true species is not very showy, with narrow petals and an odd spidery appearance. It has, however, been hybridized into spectacularly showy flower forms in a wide color range including salmon, rose, fuchsia, white, and pale pink. It grows under oaks and pines and can reach up to 36 inches in height. All clarkias are best planted thickly to support each other and give a spectacular color display.

Clarkias need no special treatment and germinate readily in two to three weeks during the cooler months. They are best sown either *in situ* in fall, before the rains begin, or in well-drained seed flats or pots. The seeds need light to germinate, so cover minimally or not at all. Do not use rich potting soil or fertilizer, as clarkias are adapted to poor soils and will bloom more freely if not overfed. They can be sown successively for extended bloom, as late as April in coastal areas. If sown directly in the ground, be sure the area is weed free. Supplemental watering will extend the bloom period. They will reseed. Seed of many clarkias can be purchased online and at the Botanic Garden Visitor Center; during the cooler months Annie's Annuals and Perennials has probably the best selection of species and named varieties available.

Purple Mouse-Ears (*Diplacus douglasii*)

A serpentine endemic, purple mouse-ears is distributed from Monterey County to the Washington border, inhabiting both the Coast Ranges and Sierra foothills as well as the Warner Mountains in northeastern California. It can be a riparian annual but is just as often found away from water, in chaparral and woodlands. The flower often overshadows the plant in size. When only one half to three inches tall, it blooms in a blaze of magenta purple, with the lower petal lobes reduced and the upper two lobes prominent, thus the common name purple mouse-ears. To ensure survival during times of stress, the plant becomes cleistogamous: instead of producing full-blown flowers, a nutrient drain, it produces small unopened flowers that self-pollinate, thus insuring seed for the next generation. Propagation of serpentine endemics requires very few nutrients in the propagation mix, and the plants should be grown in infertile

soils. They are easily overtaken by neighboring plants that thrive in fertile soil, and their success in their native habitat is mostly due to their ability to survive in soils that would be toxic to most nonserpentine endemics. Sow the seed thinly on gravelly or sandy medium, transplant when two sets of true leaves appear, and perhaps plan to enjoy the plants in pots, as their size makes them easy to overlook in the garden. If you live in an area with serpentine soils, this might be one to try, if you could find seed!

Vernon Smith



Gold nuggets mariposa-lily (*Calochortus luteus*)

Gold Nuggets Mariposa-lily (*Calochortus luteus*)

One of the easiest mariposa-lilies for the garden, *C. luteus* sends up a 30-inch branched stem with several golden yellow bowl-shaped flowers marked inside with brown dots and often a single dark spot at the base of each petal. It grows from a bulb and demands summer-dry conditions or excellent drainage. Spring flowering occurs in grasslands, open forest, and coastal prairie along the central Coast Ranges and in the Sierra foothills, with a few examples in the Central Valley. It can take part shade. It is best sown in fall, with no special seed treatment other than good drainage in the medium. Cover the seed lightly and keep it just damp. It will send up a slender leaf that grows all winter, then goes dormant in summer. Leave it in the original pot, let it dry out, and put it out again in the fall to repeat the growth pattern, and the second year it may well bloom for you. *Calochortus* are now being imported by Dutch bulb companies and can sometimes be found in retail nurseries or online. A selection called 'Golden Orb', with

larger flowers, is listed for sale from Pacific Rim Nursery. Seeds of several *Calochortus* species can often be found in the seed box at the Botanic Garden Visitor Center, depending on the year's seed collection.

Pacific Rhododendron (*Rhododendron macrophyllum*)

The Pacific rhododendron is an evergreen shrub or small tree that can often be found on disturbed sites such as logged slopes and roadcuts. It is in fact a good erosion-control shrub and grows from 7 to 30 feet tall, with enormous leaves and large showy clusters of white to pink flowers in terminal clusters. It grows on moist, well-drained, shady sites in coastal mountains from southern British Columbia to Monterey Bay in California, blooming from April to July. It is the state flower of Washington. Coast redwood, Douglas fir, and yellow pine forests are the best places to see this stunning shrub when in bloom.

The seed is formed in a small capsule at the end of summer; when the capsule turns brown and woody the seed is ripe. Take note, the seed is like dust—97,000,000 seeds per pound. Sow the seed on a perlite or peat medium with a thin layer of perlite or grit on the surface to inhibit damping off, a fungal disease. The seeds should not be covered. A product called RootShield®, available online, is a biologically safe fungicide that you can mix into solution and use to drench the seed flat before sowing it. Keep the surface moist. It takes five or more weeks to see the minute seedlings emerge, and another four months until they are large enough to move into small pots. Be prepared to watch over the little plants for two to three years before they are large enough to plant out and be sure drainage is excellent. When fungicides were still available, they were used throughout the seedling and transplant stage because damping off can wipe out the crop in a few days. RootShield® is your best option now. The plants are commercially available from mail-order growers in Washington and Oregon. The seed is short-lived and best collected from the plants you buy. 🌱

Susan Ashley has taught Propagation at Merritt College, Diablo Valley College, and the Regional Parks Botanic Garden. She has a special interest in California native plants and currently runs a small business growing natives for local retail nurseries.

Seed Banking of Two Rare Clarkias *by Rosie Andrews*

Might generations spent in cultivation lead to genetic modification in two *Clarkia* species that are extremely rare in the wild? A seed collection effort undertaken by the Regional Parks Botanic Garden staff this past fall could supply some of the genetic material needed to answer that and other questions.

Annual flowers are typically treated as ephemerals in most botanic gardens, so the garden is notable in tracking and managing self-sustaining populations of a number of annual and short-lived species that are extremely rare in the wild: Contra Costa wallflower

(*Erysimum capitatum* var. *angustatum*), Antioch Dunes evening primrose (*Oenothera deltoids* subsp. *howellii*), Milo Baker's lupine (*Lupinus milo-bakeri*), Vine Hill clarkia (*Clarkia imbricata*), and Raiche's red ribbons (*Clarkia concinna* subsp. *raichei*). All these species are narrowly distributed and considered critically imperiled in the wild but have thrived in cultivation for generations in the garden. Their vibrant annual displays are a treat for garden visitors, but they may also serve science by providing valuable genetic

material for use in conservation and research, since the garden's more forgiving growing conditions often produce robust specimens with many viable seedpods.

In the Fall 2015 issue of *Manzanita* (Vol. 19, Nos. 3 and 4), Garden Director Bart O'Brien wrote about the California Plant Rescue (CaPR), a new statewide project dedicated to long-term seed banking of California's flora. As O'Brien explained, CaPR is "a statewide coordinated effort to gather genetically representative seed collections from plant populations throughout the state as well as from northwestern Baja California, Mexico." As one of the initial participants, the garden looks for opportunities to contribute to CaPR, so after the heavy winter rains last year led to a bumper seed crop in both species of endangered clarkias in the garden, the staff decided it would be an ideal time for collection. The seeds will be stored in both the garden's seed bank and, through CaPR, at the Rancho Santa Ana Botanic Garden seed bank in

southern California, where they will remain available for research and conservation.

Why is this collection of value? In stressed wild populations, preferred methods for collecting genetically representative material often butt up against harsh realities: How does one collect no more than ten percent of the seeds available on an individual plant when only two seed pods are available? Is it practical to gather seed from 50 individuals, the recommended minimum standard? And will doing so add even more pressure to endangered species whose future is already uncertain? The constraints of gathering from wild populations makes every seed precious, so using viable seed from documented cultivated sources for experimentation can be very useful.

Clarkia imbricata, a narrow endemic, was historically found in only three locations in central Sonoma County, and now only in the Vine Hill Preserve, where it was introduced in 1974 to aid in the preservation of the species. It was first introduced to the garden in the 1960s by then-Garden Director James Roof. The plants currently on display in the Sierran rock bed originated with a 1983 collection made near Pitkin Marsh in Sonoma County, and while initially sown in heavier clay soils on the opposite side of the gardeners' nursery in the Redwood section, over time the plants migrated unassisted to their present well-drained location in a volcanic outcrop. They have thrived there for many generations, producing taller, more vigorous plants over the years, perhaps because the bed's well-drained mineral soil mix more closely resembles the acidic inland Sonoma County sands of its type location than the clay soils in the adjacent Redwood section bed.

When it came time for collecting seeds of *Clarkia imbricata*, garden aesthetics and science intersected, because Gardener Michael Uhler liked the visual effect of the dried plant skeletons and their shingle-like, overlapping leaves and requested that they be preserved in situ, rather than have the entire plant pulled. Interpretive Student Aide Kiamara Ludwig accepted the challenge, kneeling carefully to remove two average pods from each plant and drawing an inconspicuous ink band around the base of the stem to guard against double-collection, since the process required many repeat visits. The plants, with their remaining seeds, were left in place, continuing to provide visual interest and ready to self sow later in the season.

Raiche's red ribbons is known only from its type



Bart O'Brien

Clarkia concinna subsp. *raichei*

locality south of Tomales but has been grown for several years in the garden in the upper bulb bed by the glasshouse, at the northern edge of the Santa Lucia section. Even smaller than the typical *Clarkia concinna*, this diminutive, self-pollinating plant is seldom taller than three inches, with seed production often limited to just a couple of pods per plant. Gathering its seeds was simplified somewhat because the entire population was collected—entire dried plants were carefully pulled rather than selecting individual pods. Interpretive Student Aide Chris McCarron collected, cleaned, and packaged the seeds, and, since this was a full removal of all the plants, McCarron set aside half the collected seeds for seed banking and kept half for sowing in the garden to continue our population.

When gathered for seed banking, seed from each individual plant is carefully cleaned and stored separately. The plant is examined for any notable characteristics and relevant descriptive data (such as the size of the seed set and the specimen and the presence

of fungus or evidence of plant disease) is recorded to accompany seeds to their banking location for future reference. Once harvested, cleaned, and tested for viability, the collected seeds will be stored at both the garden and long-term storage through the California Plant Rescue Project (CaPR) at the Rancho Santa Ana Botanic Garden.

How might these stored seeds be of use in the future? Restoration of a lost population is one obvious use, but Garden Director Bart O'Brien posed another: it would be an interesting research topic to investigate whether generations in cultivation have led to any genetic variation (aka genetic drift) from the wild species, and if so, how much. Wild-collected seed from both Raiche's red ribbons and Vine Hill clarkia were gathered the same season by the University of California Botanical Garden to be banked through CaPR, so all the material is in place, waiting for an inquiring mind to seek answers. 🌱

Rosie Andrews has been a docent at the garden since 2009 and is currently Publications Chair of Manzanita.



Sieves (upper left) of all different screen sizes are used to sort and clean seeds and even spores. Packets (upper right) contain all the seeds from the 285 *Clarkia concinna* subsp. *raichei* plants that were growing in the garden last year. There are eight rubber-banded groups: four groups will be sent to the seed bank and four will stay in the garden. The paper plate (lower left) demonstrates how low-tech seed cleaning can be. A close-up of that paper plate (lower right) shows the seeds (the larger dark objects) and the smaller debris fragments which are discarded before the seeds are packaged.

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A special opportunity to tour the Botanic Garden and hear from docents, volunteers, *Friends*, and staff about California's spectacular plant diversity, natural history, and ethnobotany.

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Thank You to these Nurseries for Providing a Discount to *Friends* Members

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Annie's Annuals and Perennials (510-215-3301), 740 Market Avenue, Richmond, www.anniesannuals.com

Bay Natives Nursery (415-287-6755), 10 Cargo Way, San Francisco, www.baynatives.com

Berkeley Horticultural Nursery (510-526-4704), 1310 McGee Avenue, Berkeley, www.berkeleyhort.com

California Flora Nursery (707-528-8813), 2990 Somers Street at D Street, Fulton (north of Santa Rosa), www.calfloranursery.com

Central Coast Wilds (831-459-0655), 336 Golf Club Drive, Santa Cruz, www.centralcoastwilds.com (please call before visiting)

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